

Daily and Seasonal Patterns in Abdominal Color in *Diaphorina citri* (Hemiptera: Psyllidae)

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ABSTRACT *Diaphorina citri* Kuwayama, a psyllid vector of huanglongbing (citrus greening disease), exhibits three more or less distinct abdominal colors in the adult psyllid: gray/brown, blue/green, and orange/yellow. We explored the daily (in individuals in the laboratory) and seasonal (in a field population) patterns in abdominal color of adult *D. citri* to clarify the biology of this species in relation to abdominal color and investigated the relationship between abdominal color and the reproductive state of adults (i.e., whether an individual is reproductively mature, has mated, or—in females—is gravid). Females were predominantly blue/green throughout their lives, with a small portion of individuals being gray/brown, especially just after emergence. Approximately 86% of mated females developed an orange/yellow abdominal color after mating, but they ultimately turned back to blue/green within several days to 1 mo after mating. Only 31% of virgin females turned orange/yellow. Males were predominantly blue/green early in life, but a greater portion of males relative to females were gray/brown. The orange/yellow color in females reflected the presence of eggs in the abdomen; in males it seemed to derive from the color of the internal reproductive organs, and it was generally only evident in older males. The preponderance of blue/green females, rarity of gray/brown females relative to gray/brown males, and rarity of orange/yellow males and females was largely reflected in sticky card trap captures from the field. Abdominal color is of essentially no value in discerning the state of sexual maturity and of only limited value in discerning whether females have mated.

KEY WORDS Asian citrus psyllid, body color, pigment, reproductive state, huanglongbing

The psyllid *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) vectors three phloem-restricted, noncultured bacteria in the genus “*Candidatus Liberibacter*,” the causative agents of huanglongbing (citrus greening disease) (Halbert and Manjunath 2004, Hung et al. 2004, Bové 2006). First found in Florida in June 1998 (Tsai et al. 2000), *D. citri* has since spread throughout the state’s citrus-growing regions (Michaud 2004). *D. citri* may cause direct feeding damage (Michaud 2004), but the primary economic importance of the psyllid is transmission of huanglongbing, one of the world’s most serious diseases of citrus (Bové 2006). Huanglongbing was first found in southern Florida in August 2005, and only “*Candidatus Liberibacter asiaticus*” is known to occur in the state (Bové 2006). Citrus trees infected by this disease may live only 5 to 8 yr, during which time they produce misshapen, poorly colored, bitter-tasting, unmarketable fruit (Halbert and Manjunath 2004, Bové 2006). Despite the great economic importance of *D. citri* as a vector

of huanglongbing, relatively little is known about the basic biology and ecology of this pest.

Variation in body color has been described in numerous species in the Sternorrhyncha, and the clarification of the biological and ecological significance of such color polymorphisms remains an active area of research. Color variation in psyllids is generally associated with different seasonal forms in which the winter morphotype is darker, which presumably has a thermoregulatory function. Examples include the pear psylla, *Cacopsylla pyricola* (Förster) (Wong and Madson 1967, Krysan and Higbee 1990); *Cacopsylla mitoriae* (Miyatake) (Inoue 2004); *Cacopsylla elegans* Inoue (Inoue 2004); *Cacopsylla chinensis* (Yang & Li) (Yang et al. 2004); and *Agonoscyta pistaciae* Burckhardt & Lauterer (Mehrnejad and Copland 2005). Similar seasonal variation in body coloration also has been described in many species in the Aphididae (e.g., Watt and Hales 1996; Stoetzel and Miller 1998, 2001; Toros et al. 2003). Color polymorphisms in psyllids and aphids have generally been described in populations over time rather than at the level of individuals, and individual body color may not be dynamic for many species (but see Nevo and Coll 2001).

Confusion has surrounded the characterization of different abdominal colors observed in *D. citri*, par-

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ticularly regarding the relationship between abdominal color and reproductive state. Inconsistent terminology to describe what is apparently the same color category may contribute to the confusion. For example, Husain and Nath (1927) described the three categories of abdominal colors found in *D. citri* to be "grayish brown," "bluish," and "orange," whereas Skelley and Hoy (2004) used the terms "tan," "green," and "orange." Hoffman (1933) and Pande (1971) described the abdominal color of *D. citri* only as "dark brown" and "brown-gray," respectively. Tsai and Liu (2000) did not refer to adult colors, but they stated that the abdomens of mature nymphs turn either "bluish green" or "pale orange."

Despite the variation in terminology, there seems to be some agreement on the distinction of three broad color categories in *D. citri*. Based on previous work (Husain and Nath 1927, Tsai and Liu 2000, Skelley and Hoy 2004) and on our own observations, we recognize three more or less discrete color classifications, each of which includes a range of gradations between two colors: gray/brown, blue/green, and orange/yellow. Gray/brown individuals in particular show the most variation in hue, in part because the cuticle of the insect may be brown but covered to varying degrees by white scales, yielding an overall gray appearance in some individuals (Husain and Nath 1927). Additionally, color changes may take 1–2 d (E.J.W., unpublished data) and individuals undergoing a color change often exhibit a mosaic of more than one color—most notably when some blue/green females change to orange/yellow as they produce eggs.

The change in abdominal color of adult *D. citri* to yellow or orange has been thought to reflect reproductive state. For example, Husain and Nath (1927) reported that the abdomen is usually orange in gravid females, and more recently, Halbert and Manjunath (2004) stated that the female's abdomen turns orange when egg laying is imminent. Skelley and Hoy (2004) equated reproductive maturity with a change in abdominal color from green to orange, stating that both males and females reach reproductive maturity (i.e., turn orange) ≈ 20 d after emerging as adults. We have recently confirmed that adults of both sexes reach reproductive maturity at 2–3 d after eclosion (Wenninger and Hall 2007)—which is more consistent with reports of adults mating within hours to a few days after emergence (Husain and Nath 1927, Pande 1971)—and we have observed that females with blue/green abdomens are capable of laying fertile eggs (E.J.W., unpublished data).

The different abdominal color morphs in *D. citri* are not associated with other clear differences in morphology, and the abdominal color generally changes over the life of an individual. Thus, the color polymorphisms seem not to represent seasonal morphs as are found in many sternorrhyncan species in more temperate climates (see above). Many insects exhibit a green or blue/green body color due to a mixture of yellow pigment (including carotenoids) and blue bile pigments (Cromartie 1959, Law and Wells 1989, Saito et al. 1998). The orange/yellow and blue/green col-

oration found in *D. citri* may be due to the presence of carotenoids and blue bile pigments, which may be present in the epidermal cells and/or the hemolymph of insects (Barbier 1981, Law and Wells 1989, Saito et al. 1998).

We performed laboratory studies with *D. citri* to examine the lifetime dynamics in abdominal color in mature nymphs and virgin and mated adults to clarify any relationship between abdominal color and reproductive state. We also compared the mass of psyllids of different sex and abdominal color. Additionally, we sampled adult *D. citri* in citrus with yellow sticky cards to examine the seasonal variation of the relative abundance of individuals in the field having a given abdominal color. The goal of these studies was to clarify the reproductive biology and ecology of *D. citri* in relation to abdominal color.

Materials and Methods

Daily Patterns in Abdominal Color. All adult psyllids used in experiments were collected as fifth instars from a laboratory colony reared on *Murraya paniculata* (L.) Jack at the United States Horticultural Research Laboratory, as described by Hall et al. (2007). We transferred fifth instar nymphs individually to *M. paniculata* seedlings (2–3-leaf stage) caged in plastic vial containers, described in Wenninger and Hall (2007). Briefly, each cage consisted of a 52-mm-tall vial, modified as an open-ended cylinder with a foam plug used to stopper the top opening and two ventilation holes on the sides; individual cages were slipped over a seedling grown in a cone-shaped planting container. Until ready for use in experiments, adult psyllids were held in an environmental chamber at 26°C, 60% RH, and a photoperiod of 14:10 (L:D) h, which resulted in 70–80% RH inside the vials. Light intensity (from fluorescent lights) just above the plastic vial containers was $\approx 3,200$ lux. Every 24 h until they died, we examined each psyllid, recording the day that each nymph eclosed as an adult and the abdominal color. Each psyllid was assigned to one of the three more or less distinct color categories (gray/brown, blue/green, or orange/yellow) or to two intermediate categories (gray/brown to blue/green or blue/green to orange/yellow) based on the color of the ventral side of the abdomen.

All of the males observed ($n = 41$) and about half ($n = 70$) of the 127 females observed were used in mating studies in which males and females at 3–7 d postemergence were paired for at least 24 h and no more than 2 wk and isolated thereafter (Wenninger and Hall 2008). The remaining females ($n = 57$) were left unmated. To provide new oviposition sites, all mated females (and 13 of the virgin females) were transferred to a new seedling four times at 4–5-d intervals; thereafter, each female was maintained on the same seedling for the duration of her life. The remaining virgin females and all males (after mating) were maintained on the same seedling for the duration of their lives. All psyllids were held on individual seedlings that were matched as far as possible for age

Table 1. Comparison of wet mass (mean \pm SEM) of colony-collected *D. citri* among sex and abdominal color combinations

Sex	Abdominal color	n	Psyllid mass (mg)
Female	Gray/brown	42	0.343 \pm 0.013a
Female	Blue/green	34	0.486 \pm 0.023c
Female	Orange/yellow	34	0.545 \pm 0.020d
Male	Gray/brown	37	0.337 \pm 0.014a
Male	Blue/green	22	0.410 \pm 0.022b

Means within a column followed by the same letter are not significantly different ($\alpha = 0.05$; Tukey's pairwise comparisons test).

and development of flush (immature leaves as described by Hall and Albrigo 2007); development of plants was slow enough that flush was constantly available to psyllids for the duration of the experiment regardless of whether they were transferred to new seedlings. After all psyllids died, we graphically examined patterns of daily changes in abdominal color of the three groups of psyllids observed (virgin females, mated females, and mated males).

Psyllid Mass in Relation to Abdominal Color. From our laboratory colony, we collected *D. citri* adults \approx 7–10 d after eclosion and determined the sex and abdominal color of each individual. We obtained the following color and sex combinations: gray/brown, blue/green, and orange/yellow females; and gray/brown and blue/green males (see Table 1 for sample sizes); we were unable to find any orange/yellow males on the collection date. Only psyllids that could be readily assigned to a distinct color category were used (i.e., no gray/brown to blue/green or blue/green to orange/yellow psyllids were used). Immediately after sexing psyllids, they were placed in a freezer and held there overnight. We then measured the wet mass of each psyllid to the nearest 0.01 mg. The data were normally distributed (based on Kolmogorov-Smirnov test and examination of residual plots), but variances were not equal (Levene's test); therefore, we used weighted least squares analysis of variance (ANOVA) to compare body mass among the five color and sex combinations. Weights were calculated using the absolute value of each residual ($|e_i|$) from ordinary least squares ANOVA as an estimate of standard deviation (σ_i); each observation was then weighted by the reciprocal of the estimate of its variance ($1/\sigma_i^2$). Tukey's pairwise comparisons test was used to discriminate among means.

Seasonal Patterns in Abdominal Color. We deployed yellow sticky cards in citrus to sample adult psyllids and examine the seasonal patterns in the relative abundance of individuals of different abdominal color. The study was conducted in a block of 'Hamlin' orange trees (*Citrus sinensis* L.; 4 yr old, \approx 2 m tall) in a USDA-ARS grove near Fort Pierce, FL (Saint Lucie County). No systemic or foliar insecticides were applied before or during the course of the study. Yellow sticky traps (7.62 by 12.7 cm; sticky on both sides; a bright yellow hue similar to S-G-390 by Behr Process Corp., Santa Ana, CA) were obtained from Great Lakes IPM (Vestaburg, MI). One trap per tree was

placed in each of 10 trees randomly selected across the block of trees. Traps were suspended 1–1.5 m above ground near the outside of the canopy from a branch by using a black twist tie (178 mm length, Multi-Purpose Tie/UV; Thomas and Betts Corp., Memphis, TN). The traps were deployed in the field for 1-wk durations at biweekly intervals over 52 wk, beginning on 4 January 2005. After collection from the field, traps were stored in a freezer in the laboratory. The number of adult psyllids of each sex and color (only the three distinct categories were used: gray/brown, blue/green, or orange/yellow) combination per trap was tabulated for each wk. Data were analyzed using a separate 2 by 2 chi-square contingency table (Quinn and Keough 2002) for each week (because so few orange/yellow individuals were collected on sticky cards, this color category was not included in the analysis). For cases in which the expected count within one or more cells was <5 , we used Fisher exact test rather than chi-square.

Before collecting seasonal sticky card data, we performed a pilot study in which we placed psyllids of known abdominal color on sticky cards, left them in the field for 1 wk, and then we transferred them to a freezer for 24 h and determined whether individuals retained their original abdominal color (E.J.W., unpublished data). Gray/brown individuals were easily recognized, but many orange/yellow individuals that initially had a more yellow appearance became clearly orange (but still distinct from other color categories). Many individuals that were initially blue/green were predominantly gray/brown after freezing, with only the anterior portion of the abdomen remaining distinctly blue/green; therefore, such individuals were categorized as blue/green.

Results

Daily Patterns in Abdominal Color. Fig. 1 presents results for observations on the daily color of adults through 70 d after eclosion, but 12 of the 57 virgin females observed and 10 of the 70 mated females observed lived beyond 70 d (some for 100 d or longer), staying blue/green for the remainder of their lives. The two males that lived beyond 70 d were either orange/yellow or gray/brown until death. On the day preceding adult eclosion, \approx 64% of female nymphs and 70% of male nymphs were blue/green, with the remaining individuals exhibiting the "pale orange" coloration mentioned by Tsai and Liu (2000) (Fig. 1). After adult eclosion, the portion of female psyllids with a gray/brown abdomen gradually diminished and stabilized to \approx 5–10%, reflecting for the most part a small number of females that remained gray/brown until death (Fig. 1A and B). Beginning at 5 d after eclosion, the portion of virgin females with an orange/yellow or blue/green to orange/yellow abdomen increased and ultimately fluctuated \approx 3–8%; \approx 33% of virgin females had some degree of orange/yellow coloration at some point in their lives, but few individuals exhibited the color at any given age (Fig. 1A). All virgin females were blue/green by 60 d after eclosion

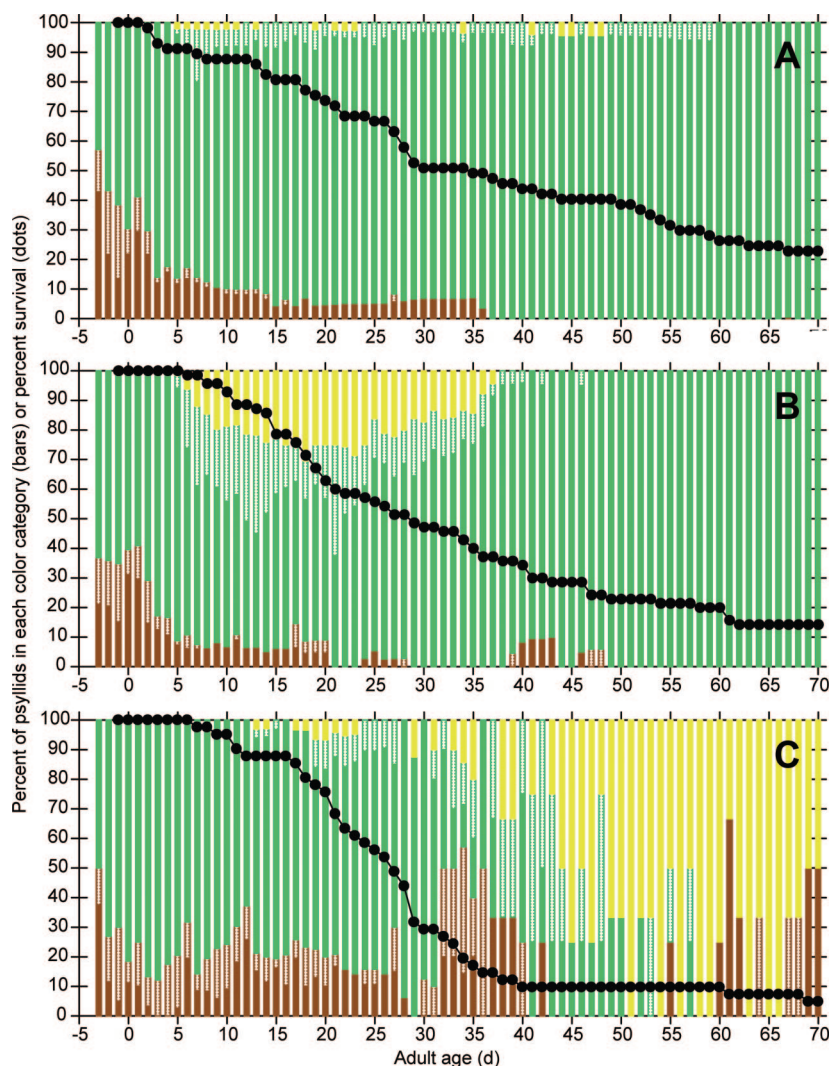


Fig. 1. Daily changes in abdominal color and adult survival for virgin female (A), mated female (B), and mated male (C) *D. citri*. Initial sample sizes were 57, 70, and 41, respectively. Age "0 d" represents the day of adult eclosion. Mated psyllids were paired for between 24 h to 2 wk beginning at 3–7 d after eclosion. Bar color corresponds to abdominal color as follows: brown, gray/brown; stippled brown, gray/brown to blue/green; green, blue/green; stippled green, blue/green to orange/yellow; yellow, orange/yellow. For simplicity, nymphs (age -3, -2, -1 d) that were pale orange were categorized in the gray/brown group.

and through the remainder of their lives. For mated females, the portion of individuals with an orange/yellow or blue/green to orange/yellow abdomen increased sharply at 6–7 d after eclosion and peaked $\approx 40\text{--}60\%$ $\approx 12\text{--}21$ d after eclosion (Fig. 1B). Across days 6–37 after emergence, $32.5 \pm 1.9\%$ (mean \pm SEM) of mated females were orange/yellow or blue/green to orange/yellow (Fig. 1B). A greater percentage of mated females (86%) relative to virgins exhibited an orange/yellow abdominal hue at some point in their lives, but by 49 d after eclosion and for the remainder of their lives, the abdominal color of all mated females was blue/green. Of the females that turned orange/yellow or blue/green to orange/yellow, the mean \pm SEM age at which the abdomen

changed color was 9.0 ± 0.5 d after eclosion (4.0 ± 0.5 d after mating) for mated females ($n = 60$) and 10.7 ± 1.7 d after eclosion for virgin females ($n = 19$).

Males showed more variation in abdominal color (Fig. 1C). Compared with females, a greater portion of males were gray/brown or gray/brown to blue/green, and they tended to remain so for longer periods. Males of orange/yellow abdominal color were observed at a very low frequency until around 40 d after eclosion when the orange/yellow color category gradually became the dominant color observed. Of the few males that lived beyond 57 d, none exhibited any blue/green coloration. We did not observe an obvious change in abdominal color of males that could be linked with the timing of mating (age 3–7 d). Neither

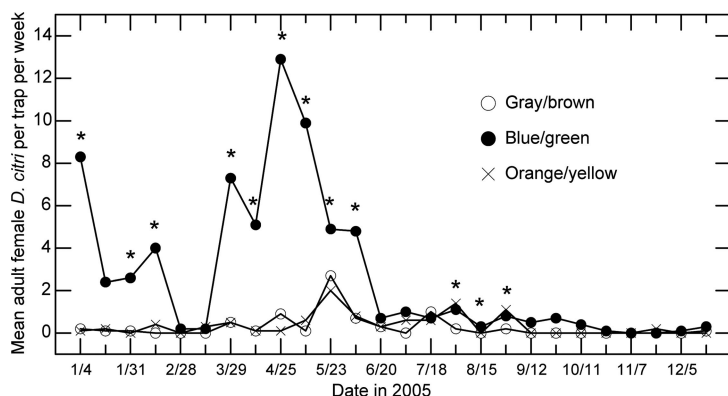


Fig. 2. Mean number of adult female *D. citri* per yellow sticky card per wk, separated by abdominal color. Traps were deployed in the field for 1-wk durations at biweekly intervals beginning on 4 January 2005. Asterisks indicate wk in which the observed total frequency of blue/green and gray/brown females was greater than or less than, respectively, expected frequencies based on chi-square tests on contingency table data (see Table 2). Analyses were not performed for 7 November, 21 November, or 5 December in which three cells contained frequencies of zero.

males nor females showed an obvious change in abdominal color that corresponded with the onset of reproductive maturity (2–3 d after emergence).

Female lifespan was reduced in the mating treatment that featured multiple males housed with individual females for 2 wk (Wenninger and Hall 2008). With this treatment excluded, female longevity did not differ between virgin (mean \pm SEM, 45.1 ± 4.8) and mated (42.8 ± 4.3) females ($t = -0.36$, $df = 113$, $P = 0.721$; t -test). However, male longevity (28.2 ± 2.5 d) was significantly lower than that of overall female longevity (43.9 ± 3.2) ($t = 2.8$, $df = 154$, $P = 0.005$; t -test).

Psyllid Mass in Relation to Abdominal Color. Psyllids of different color and sex combination differed significantly in body mass ($F = 1,055.2$; $df = 4, 163$; $P < 0.0001$) (Table 1). Gray/brown females and males did not differ significantly from each other but had lower mass than the other three groups, which each differed significantly among each other. The mass of gray/brown females was $\approx 30\%$ lower than that of blue/green females, and for gray/brown versus blue/green

males the difference was $\approx 18\%$. Orange/yellow females had the greatest mass, followed by blue/green females and blue/green males; the mass of blue/green females was $\approx 11\%$ lower than that of orange/yellow females.

Seasonal Patterns in Abdominal Color. The total abundance of males and females collected on yellow sticky cards was remarkably similar over the course of the yr (Figs. 2 and 3). Blue/green individuals (both male and female) were generally more abundant than gray/brown individuals; however, based on chi-square tests on contingency table data (Table 2), there were typically more blue/green relative to gray/brown females than expected and fewer blue/green relative to gray/brown males than expected. In fact, for each week in which the observed and expected frequencies differed significantly, blue/green females and gray/brown males occurred in frequencies that were greater than expected by chance. Orange/yellow individuals—notably males—were rarely found on sticky cards (Fig. 3), but orange/yellow females were more abundant than at any time of the year 2 wk after

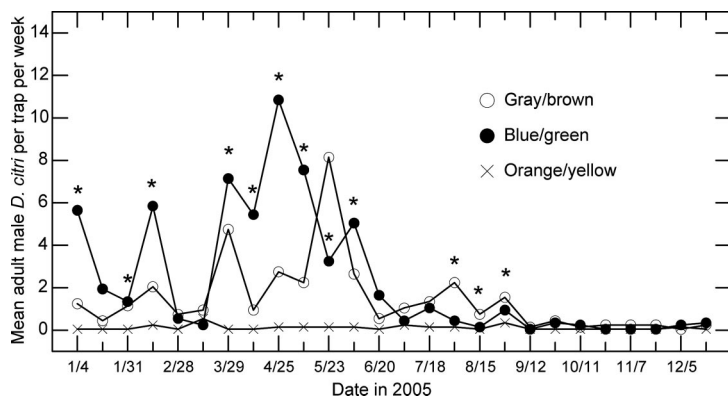


Fig. 3. Mean number of adult male *D. citri* per yellow sticky card per week, separated by abdominal color. Additional notes as in Fig. 2.

Table 2. Two-way contingency tables showing the total and expected (in parentheses) counts of male and female *D. citri* with gray/brown and blue/green abdominal color collected across 10 yellow sticky cards on each sample date in 2005

	4 Jan. (week 1)		18 Jan. (week 3)		31 Jan. (week 5)		14 Feb. (week 7)	
	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green
Female	2 (7.8)	83 (77.2)	1 (2.6)	24 (22.4)	1 (6.4)	26 (20.6)	0 (6.8)	40 (33.2)
Male	12 (6.2)	56 (61.8)	4 (2.4)	19 (20.6)	11 (5.6)	13 (18.4)	20 (13.2)	58 (64.8)
	$\chi^2 = 10.6, P = 0.001$		$\chi^2 = 2.3, P = 0.129$		$\chi^2 = 12.5, P < 0.001$		$\chi^2 = 12.4, P < 0.001$	
	28 Feb. (week 9)		14 Mar. (week 11)		29 Mar. (week 13)		11 April (week 15)	
	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green
Female	0 (1.0)	2 (1.0)	0 (1.4)	2 (0.6)	5 (20.7)	73 (57.3)	1 (4.5)	51 (47.5)
Male	7 (6.0)	5 (6.0)	9 (7.6)	2 (3.4)	47 (31.3)	71 (86.7)	9 (5.5)	54 (57.5)
	$P = 0.462$		$P = 0.077$		$\chi^2 = 26.9, P < 0.001$		$P = 0.022$	
	25 April (week 17)		9 May (week 19)		23 May (week 21)		6 June (week 23)	
	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green
Female	9 (18.2)	129 (119.8)	1 (11.7)	99 (88.3)	27 (43.4)	49 (32.6)	7 (13.9)	48 (41.1)
Male	27 (17.8)	108 (117.2)	22 (11.3)	75 (85.7)	81 (64.6)	32 (48.4)	26 (19.4)	50 (56.9)
	$\chi^2 = 10.8, P = 0.001$		$\chi^2 = 22.4, P < 0.001$		$\chi^2 = 24.3, P < 0.001$		$\chi^2 = 7.8, P = 0.005$	
	20 June (week 25)		5 July (week 27)		18 July (week 29)		1 Aug. (week 31)	
	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green
Female	3 (2.6)	7 (7.4)	0 (4.2)	10 (5.8)	10 (9.8)	7 (7.2)	2 (8.0)	11 (5.0)
Male	5 (5.4)	16 (15.6)	10 (5.8)	4 (8.2)	13 (13.2)	10 (9.8)	22 (16.0)	4 (10.0)
	$P = 1.00$		$P < 0.001$		$\chi^2 = 0.02, P = 0.884$		$\chi^2 = 17.6, P < 0.001$	
	15 Aug. (week 33)		29 Aug. (week 35)		12 Sept. (week 37)		26 Sept. (week 39)	
	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green
Female	0 (1.9)	3 (1.1)	2 (5.0)	8 (5.0)	0 (0.8)	5 (4.2)	0 (2.0)	7 (5.0)
Male	7 (5.1)	1 (2.9)	15 (12.0)	9 (12.0)	1 (0.2)	0 (0.8)	4 (2.0)	3 (5.0)
	$P = 0.024$		$\chi^2 = 5.1, P = 0.024$		$P = 0.167$		$P = 0.07$	
	11 Oct. (week 41)		26 Oct. (week 43)		(week 45, 47, 49) ^a		19 Dec. (week 51)	
	Gray/ brown	Blue/ green	Gray/ brown	Blue/ green	(zero frequencies in three cells)		Gray/ brown	Blue/ green
Female	0 (0.6)	4 (3.4)	0 (0.7)	1 (0.3)			1 (1.3)	3 (2.7)
Male	1 (0.4)	2 (2.6)	2 (1.3)	0 (0.7)			2 (1.7)	3 (3.3)
	$P = 0.429$		$P = 0.333$				$P = 1.00$	

For cases in which the expected count within one or more cells was < 5 , Fisher's exact test rather than chi-square was used to determine whether the observed frequencies differed significantly from expected frequencies. Sample dates indicate the date traps were deployed; traps were retrieved 7 d later.

^a For week 45, 47, and 49, the data were not analyzed because three cells contained frequencies of zero.

the springtime peak total abundance of psyllids (Fig. 2).

Discussion

Color polymorphisms in psyllids and aphids have generally been described at the population level rather than in individuals (Wong and Madsen 1967; Krysan and Higbee 1990; Horton 1993; Watt and Hales 1996; Stoetzel and Miller 1998, 2001; Toros et al. 2003; Inoue 2004; Yang et al. 2004). For many species, individual variation in body color may not be dynamic (but see Nevo and Coll 2001). The variation in abdominal color that we describe in *D. citri* occurs at the level of the individual and seems not to reflect seasonal morphotypes, but rather the contents of the abdomen (Husain and Nath 1927). Moreover, the color variants are not associated with any other obvious differences in morphology, as occurs in the pear psylla, for example (Wong and Madsen 1967, Krysan and Horton 1991). Although the relative abundance of different color forms did vary over the season, psyllids from each of the different color categories that we observed may generally be found at some level over much of the year. Because seasonal morphotypes are generally associated with summerforms and overwintering win-

terforms (see Introduction), seasonal morphotypes might not be expected in a tropical to subtropical psyllid species.

The results of our study show that male and female *D. citri* differ notably in daily and seasonal patterns of abdominal color. However, abdominal color is of essentially no value in discerning the state of sexual maturity and of only limited value in discerning whether females are mated. Females often, but not always, exhibited a change in abdominal color to orange/yellow after mating, whereas males showed no change in abdominal color that could be clearly linked with mating (although we did not monitor unmated males). Such a change in the abdominal color of females after mating is not surprising given that the orange/yellow coloration is associated with the presence of eggs in the female's abdomen (Husain and Nath 1927; Halbert and Manjunath 2004), especially for females that are exhibiting high oviposition rates (E.J.W., unpublished data). Because one third of virgin females exhibited a change in abdominal color to orange/yellow, the use of abdominal color as an indicator of reproductive state in female *D. citri* can be implemented only with caution. Skelley and Hoy (2004) stated that both male and female *D. citri* exhibit a change in abdominal color (to orange) at ≈ 20 d after

adult emergence, reflecting the onset of reproductive maturity. Not only did we not observe such a change in our observations of daily color dynamics, but we also have shown that males and females reach reproductive maturity at 2–3 d after eclosion (Wenninger and Hall 2007).

The abdominal color of most individuals of both sexes is at least partly blue/green for much of their lives, with a small portion of individuals exhibiting a gray/brown abdominal color on each day, especially early in life; however, gray/brown abdominal color is more frequently observed in males than in females. We speculate that a change in abdominal color from gray/brown to blue/green is associated with feeding activity and might be related to the quantity of food ingested or whether psyllids are feeding on flush or mature leaves. The patterns that we observed in psyllid mass in relation to sex and color combinations are consistent with a relationship between feeding and abdominal color; within each sex, blue/green individuals were heavier than psyllids that were gray/brown. Attempts to test whether a change in abdominal color to gray/brown can be induced by starvation have been largely unsuccessful (E.J.W., unpublished data), because *D. citri* does not survive long off of a host plant (McFarland and Hoy 2001).

The relationship of abdominal color at mating with reproductive output in *D. citri* remains to be thoroughly investigated, but we have found that gray/brown females lay significantly fewer eggs than blue/green females in the initial days after mating, although total fecundity may not differ (E.J.W., unpublished data). Interestingly, a small portion of females in the current study maintained a gray/brown abdominal color for as long as 35–36 d (Fig. 1A), but the abdominal color of mated gray/brown females ultimately usually changes to blue/green or orange/yellow (Fig. 1B; E.J.W., unpublished data). It remains unclear why some females maintain a gray/brown abdominal color for extended periods.

The relative abundance of psyllids of different abdominal color that we observed in the laboratory was largely reflected in the sex and color combinations found on sticky cards. For both sexes, psyllids of blue/green abdominal color were generally the most abundant, consistent with the generally large frequency of this color category for psyllids maintained in the laboratory. Moreover, the greater than expected frequency of blue/green females and gray/brown males collected on sticky cards was consistent with the greater abundance of gray/brown males relative to gray/brown females in the laboratory-maintained psyllids. However, during several wk the abundance of males that were gray/brown relative to those that were blue/green was greater than would be expected based on the laboratory data in which, among psyllids under 30 d of age, only ≈ 10 –20% were gray/brown. Assuming the relative abundance of gray/brown males in our laboratory data are representative of the field population, a greater than expected capture rate of gray/brown males suggests that these males were more active dispersers. Whether a high relative abun-

dance of gray/brown males on sticky cards reflects greater dispersal or a greater relative abundance of this color category in the field remains to be examined. Psyllids of orange/yellow abdominal color—especially males—were rarely found on sticky cards. This pattern likely reflects the relative rarity of this color form in both sexes. Moreover, males in the lab exhibited orange/yellow coloration generally only after reaching an above-average age; in the field, male survival beyond 30–40 d might be even rarer. The scarcity of orange/yellow females on sticky cards also might reflect more limited dispersal tendencies in gravid females. Fully gravid females in the field and in laboratory colonies are more likely to walk than fly away when physically disturbed (Skelley and Hoy 2004; E.J.W., unpublished data), possibly because they are too heavy for sustained flight or too driven to oviposit.

The goal of these studies was to develop a more thorough understanding of the biology, ecology, and behavior of *D. citri* that may facilitate more effective monitoring and management strategies. Our data suggest that the abdominal color of *D. citri* cannot be used as a reliable indicator of reproductive state for females. Several matters regarding the dynamics in abdominal color in *D. citri* require further investigation, including the underlying reasons for changes in abdominal color (particularly to and from gray/brown and blue/green), whether tendencies toward certain colors are heritable, and to what extent abdominal color relates to reproductive output in females.

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